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TROPHIC NICHE OF NORTH AMERICAN GREAT HORNED OWLS

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ABSTRACT.—The trophic niche of Great Horned Owls (*Bubo virginianus*) was summarized using 22 North American studies reporting >100 prey items each. Twenty-one of these studies were reviewed from the published literature, and one, our Montana data, is presented here for the first time. More than 92 species from four taxonomic classes have been recorded from 19 278 prey items. Mammals constituted >93.3% of prey from all studies, with six studies reporting 100% mammalian prey. Food-niche breadth ranged from 2.09–19.15 ($\bar{x}$ = 5.17) for combined studies, 2.12–19.15 ($\bar{x}$ = 6.29) for breeding seasons, and 2.09–4.72 ($\bar{x}$ = 3.50) for non-breeding seasons. Evenness values ranged from 0.408–0.840 ($\bar{x}$ = 0.620) for combined studies, 0.420–0.703 ($\bar{x}$ = 0.596) for breeding seasons, and 0.408–0.724 ($\bar{x}$ = 0.609) for non-breeding seasons. Estimated masses of individual prey species ranged between 2 and 6300 g. Birds were only a minor part of the owl diet, although a variety of species were eaten.

KEY WORDS: *diet*; *food-niche breadth*; *Great Horned Owl*; Bubo virginianus; *North America*.

Nicho trofico del Gran Buho Cornado Americano

RESUMEN.—El nicho trófico de (*Bubo virginianus*) fue compendiado usando 22 estudios norte americanos reportando >100 ítems presa cada uno. Veintiuno de esos estudios fueron revisados en la literatura publicada, y uno, nuestros datos de Montana, se presentan aquí por primera vez. Más de 92 especies de cuatro clases taxonómicas han sido registradas a partir de 19 278 ítems presa. Los mamíferos constituyeron >93.3% de presas en todos los estudios, con seis estudios reportando 100% de presas mamíferas. La amplitud del nicho alimenticio estuvieron en el rango de 2.09–19.15 ($\bar{x}$ = 5.17) para estudios combinados, 2.12–19.15 ($\bar{x}$ = 6.29) para estaciones reproductivas, y 2.09–4.72 ($\bar{x}$ = 3.50) para temporadas no reproductivas. La masa estimada de especies presa individualmente estuvo entre 2 y 6300 gr. Las aves fueron tan solo una parte menor de la dieta del búho, aunque una variedad de especies fueron consumidas.

[Traducción de César Márquez]

The Great Horned Owl (*Bubo virginianus*) is perhaps the most widely-distributed owl in North America (Houston et al. 1998, Holt et al. 1999). Numerous studies of the food habits of Great Horned Owls have been conducted in North America and it has been considered to be an opportunistic feeder. Indeed, the Great Horned Owl has been reported to have the broadest diet of any North American owl species (Marti and Kochert 1996, Houston et al. 1998). However, the owl's trophic niche has not been reviewed continent-wide. Earhart and Johnson (1970) summarized principal food habits of Great Horned Owls from published literature, but did not identify prey to the species level, provide prey numbers, or discuss their conclusions. Jaksic and Marti (1984) made comparisons between a few Neotropical and Nearctic localities, but compared owl diets from only two regions in North America. Our paper summarizes the trophic niche of Great Horned Owls from 22 North American studies; 21 from published literature, and one, our original Montana data.

Our objectives were to: (1) determine Great Horned Owl trophic niche from west-central Montana and (2) compare trophic niche among North American studies.

METHODS

In Montana, we collected pellets and prey remains annually from 10 territories in the Missoula and Mission valleys during the breeding and non-breeding seasons from 1987–95. Prey was identified using local dichotomous keys for mammals (Hoffmann and Pattie 1968) and by comparing feather and body parts of prey with museum specimens at the Philip L. Wright Zoological Museum (University of Montana). Numbers and proportions

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of prey types were then compared between breeding and non-breeding seasons for Montana. Comparisons of trophic niche were then made among other available North American data sets.

We defined trophic niche as the relationship between owls and their prey. We followed Marti's (1987) definitions for trophic diversity in which a broad food-niche breadth (FNB) has a high number of prey species, which are nearly equally distributed, and a narrow food-niche breadth has a low number of prey species unequally distributed. However, we found no method to determine the statistical significance between narrow and wide food-niche breadth. We compared owl trophic niche from 22 North American studies with >100 prey items each (Tables 1–3). We then divided these studies into breeding season and non-breeding season diets. To compare trophic niche among studies, we primarily used prey identified to the species. Prey identified to genus were included if they occurred frequently or exhibited an unusual body mass. Insects, arachnids, and unidentified reptiles, birds, and mammals were eliminated from trophic niche comparisons because they were either not identified to genus or occurred only rarely (<1%) in the diet.

Food-niche breadth (H') was calculated for each study using the antilog of the Shannon-Weiner diversity index (Marti 1987). We used this equation because it is linearly related to the number of prey categories in the sample. Evenness was calculated using Alatalo's (1981) modification of Hill's (1973) equation: Evenness = $(N_2 - 1)/(N_1 - 1)$, where $N_1 = \exp H'$ and $N_2 = 1/p_i^2$. Evenness values range from zero to one. An evenness value of one indicates prey proportions in the diet are equal. We compared food-niche breadth and evenness values from all studies as well as those from breeding and non-breeding seasons using the Mann-Whitney *U*-test (Fowler and Cohen 1990).

Spearman rank correlation (Fowler and Cohen 1990) was used to examine the relationship between the number of mammalian species and number of prey items with food-niche breadth values among studies. We did so to determine if wider food-niche breadth values were associated with increased numbers of prey or species in the diet. The Spearman rank correlation was also used to examine the relationship between number of prey items and food-niche breadth because food-niche breadth values can fluctuate with sample size, thus influencing the results.

A relative-size category of the main prey classes eaten by the owls was derived using body mass estimates of mammals (Whitaker 1992) and birds (Dunning 1984). Standard mean prey biomass estimates were not calculated based on species because of unfounding factors. For example, standard prey biomass estimates are usually derived from the adult age class and do not consider other age classes in the population. Further, mean prey biomass estimates generally give whole carcass masses and do not consider that only specific portions of some medium to large prey are eaten (Holt 1993, 1994).

RESULTS

The Montana study yielded 4350 prey items: 2696 from the breeding season and 1654 from the non-breeding season. Although collectively the owls ate a wide variety of prey ($N = 28$), they ate predominately small mammals, particularly voles (Table 1).

Table 1. The number of individual prey consumed by Great Horned Owls during breeding and non-breeding seasons in Montana from 1987–95.

SPECIES	NO. OF PREY	
	BREEDING SEASON	NON-BREEDING SEASON
Mammals		
Microtus pennsylvanicus	1264	902
Microtus montanus	1158	470
Microtus spp.	72	159
Peromyscus maniculatus	37	52
Thomomys talpoides	54	39
Ondatra zibethicus	13	14
Mustela frenata	1	1
Sylvilagus nuttallii	2	—
Tamias amoenus	—	1
Tamiasciurus hudsonicus	2	—
Glaucomys sabrinus	—	1
Birds		
Sturnus vulgaris	30	4
Phasianus colchicus	12	4
Fulica americana	6	1
Pica pica	7	1
Turdus migratorius	3	—
Colaptes auratus	2	1
Xanthocephalus xanthocephalus	12	—
Anas platyrhynchos	2	2
Anas spp.	1	—
Bombycilla spp.	1	—
Sturnella neglecta	1	—
Asio otus	1	—
Porzana carolina	1	—
Rallus limicola	1	—
Bonasa umbellus	1	—
Agelaius phoeniceus	—	1
Other		
Catostomus spp.	4	—
crayfish	6	1
squawfish	2	—
Total	2696	1654 = 4350

During the breeding season, the owls consumed 28 species of prey. Of these however, they ate predominately small mammals, especially *Microtus* voles (92.5%, $N = 2494$). During the non-breeding season, the owls ate only 16 species of prey, again consuming predominately *Microtus* voles (92.5%, *N*

Table 2. Landscape diets of Great Horned Owls in North America. Percent of prey in taxonomic classes calculated from 22 studies, representing 19 278 prey items.

	PERCENT					
NO. OF PREY	OSTEICHTHYES	CRUSTACEA	AVES	MAMMALIA	LOCATION	SOURCE
Breeding season						
2696	0.2	0.2	3.09	6.6	MT	This study
1896	—	—	—	100.0	OR	Maser & Brodie 1966
1300	—	—	1.4	98.6	ID	Marti & Kochert 1996
398	—	1.5	2.8	95.7	UT	Smith & Murphy 1973
356	0.8	—	2.2	96.9	WY	Craighead & Craighead 1969
276	3.3	—	31.5	65.2	NY, NJ, CT	Bosakowski & Smith 1992
209	—	—	—	100.0	MB	Bird 1929
142	—	9.2	20.4	70.3	MI	Craighead & Craighead 1969
119	—	—	30.3	69.7	OH	Springer & Kirkley 1978
Non-breeding season						
1845	—	—	1.4	98.6	MI	Craighead & Craighead 1969
1654	—	0.1	1.0	98.9	MT	This study
756	2.5	—	1.9	95.6	MT	Seidensticker 1968
584	—	—	0.3	99.7	CA	Rudolph 1978
210	—	—	2.4	97.6	IN	Kirkpatrick & Conway 1947
161	—	—	—	100.0	NE	Rickart 1972
122	—	—	—	100.0	YT	Weir & Hanson 1989
Breeding and non-breeding seasons						
2571	—	0.1	4.4	95.2	WI	Errington 1932
2152	—	—	1.7	98.1	CO	Marti 1974
809	0.1	—	1.7	98.1	WA	Knight & Jackman 1984
568	—	—	—	100.0	CA	Barrows 1989
273	—	0.7	21.2	78.0	WI	Orians & Kuhlman 1956
178	—	—	—	100.0	OK	Tyler & Jensen 1981

= 1531). The decreased prey species diversity during the non-breeding season reflected the fewer species of prey available during the fall and winter months in Montana.

The 22 studies combined yielded 19 278 prey items (Table 2) from eight western, six central, and three eastern states, and two Canadian provinces. Studies from New York and Pennsylvania (Latham 1950), and Alberta (Rusch et al. 1972, McInvaille and Keith 1974, Adamcik et al. 1978) were also reviewed but omitted from trophic calculations because dominant prey species were not always identified to genus or species.

The owls consumed ≥92 prey species from four taxonomic classes: Osteichthyes, Crustacea, Aves, and Mammalia (Table 2). Mammals composed ≥65.2% of the prey from each study, constituting 93.3% of the total prey from all studies. Six studies reported 100% mammalian prey (Table 2).

Although the owls preyed on a broad number of species overall, *Microtus* (N = 10 studies), *Peromyscus* (N = 6), *Perognathus* (N = 2), *Sigmodon* (N = 1), and *Lepus* (N = 1) species represented the highest percentage of prey in all studies. Overall, food-niche breadth values ranged from 2.09–19.15 ($\bar{x}$ = 5.17, SD ± 3.61) (Table 3). Food-niche breadth values for the breeding season (range = 2.12–19.15, $\bar{x}$ = 6.29, SD ± 5.39, N = 9) and non-breeding season (range = 2.09–4.72, $\bar{x}$ = 3.50, SD ± 0.82, N = 7) were similar. Food-niche breadths were not significantly different (Mann-Whitney U = 24.5, $P > 0.05$) between seasons.

The broadest food-niche breadth (FNB = 19.15) was from New York, New Jersey, and Connecticut, where 15 mammal species constituted 65.2% of the diet, with *Peromyscus* representing 14.3% (Bosakowski and Smith 1992) (Table 3). Fourteen other mammal, 20 bird, and two fish species comprised the remainder. The broad FNB in this study, compared to other studies, may be explained by the

Table 3. Trophic parameters calculated from twenty-two studies representing 19 278 prey items.

No. of Prey	Food-niche Breadth	Evenness	Location	Source
Breeding season				
2696	3.27	0.644	MT	This study
1896	2.12	0.465	OR	Maser & Brodie 1966
1300	8.12	0.686	ID	Marti & Kochert 1996
398	4.47	0.420	UT	Smith & Murphy 1973
356	2.85	0.566	WY	Craighead & Craighead 1969
276	19.15	0.670	NY, NJ, CT	Bosakowski & Smith 1992
209	2.94	0.687	MB	Bird 1929
142	4.55	0.527	MI	Craighead & Craighead 1969
119	9.10	0.703	OH	Springer & Kirkley 1978
Non-breeding season				
1845	2.94	0.669	MI	Craighead & Craighead 1969
1654	3.43	0.649	MT	This study
756	3.91	0.622	MT	Seidensticker 1968
584	2.09	0.724	CA	Rudolph 1978
210	4.72	0.631	IN	Kirkpatrick & Conway 1947
161	3.84	0.558	NE	Rickart 1972
122	3.56	0.408	YT	Weir & Hanson 1989
Breeding and non-breeding season				
2571	4.89	0.629	WI	Errington 1932
2152	6.36	0.605	CO	Marti 1974
809	5.27	0.602	WA	Knight & Jackman 1984
568	3.89	0.840	CA	Barrows 1989
273	6.98	0.604	WI	Orians & Kuhlman 1956
178	5.87	0.720	OK	Tyler & Jensen 1981

large number of bird, as well as mammal, species included in the diet, or the relatively small sample size ($N = 276$).

Food-niche breadth calculated from Ohio (Springer and Kirkley 1978) was also broad (9.10) compared to other studies (Table 3). In this study, six mammal species constituted 69.7% of the owl's diet with *Microtus* representing 26.1%. Six mammal and 12 bird species represented the remainder of the diet. The narrowest FNBs came from California (2.09), Oregon (2.12), Wyoming (2.85) and Manitoba (2.94), respectively (Table 3). In all these cases, small mammals dominated the diet (Bird 1929, Maser and Brodie 1966, Craighead and Craighead 1969, Rudolph 1978).

Evenness values overall ranged from 0.408–0.840 ($\bar{x} = 0.620$, SD $\pm$ 0.101). Evenness values for the breeding (range = 0.420–0.703, $\bar{x} = 0.596$, SD $\pm$ 0.105, $N = 9$) and non-breeding season (range = 0.408–0.724, $\bar{x} = 0.609$, SD $\pm$ 0.102, $N = 7$) were also similar (Table 3). Evenness was not significantly different (Mann-Whitney $U = 30$, $P > 0.05$) between seasons.

A weak positive correlation existed between the number of mammalian species in the diet and food-niche breadth values ($r_s = 0.299$, $P < 0.01$). A weak negative relationship occurred between the number of prey items and food-niche breadth values ($r_s = -0.207$, $P > 0.01$), suggesting that sample sizes were not influencing the results.

Mammal prey biomass ranged from 2 g, (masked shrew [*Sorex cinereus*]) to 6300 g, (striped skunk [*Mephitis mephitis*]) (Whitaker 1992). The majority of prey ranged from 2–1800 g and included shrews, voles, mice, rats, pocket gophers, squirrels, and rabbits. The dominant prey from each study, *Microtus*, *Peromyscus*, *Perognathus*, *Sigmodon*, and *Lepus* ranged in body mass from 16–85 g, 10–43 g, 16–47 g, 80–120 g, and 1800–3600 g, respectively (Whitaker 1992). Other medium-sized mammals, including yellow-bellied marmot (*Marmota flaviventris*) and white-tailed jackrabbit (*Le-*

pus townsendii) rarely occurred in the diet and ranged from 2200–4500 g.

Birds were not a major part of the owl's diet, but a wide variety of species were eaten. Waterfowl, shorebirds, pheasants and allies, and passerines represented the majority of bird prey. Several owl species were also reported as prey in nine studies: Northern Saw-whet Owl (*Aegolius acadicus*) (Bosakowski and Smith 1992), Long-eared Owl (*Asio otus*) (Marti 1976, Holt this study), Barn Owl (*Tyto alba*) (Knight and Jackman 1984), and Eastern Screech-Owl (*Otus asio*) (Errington 1932, Orians and Kuhlman 1956, Craighead and Craighead 1969, Bosakowski and Smith 1992). Body masses of avian prey ranged from: 318–1100 g, waterfowl; 74–415 g, shorebirds; 178–1317 g, pheasants and allies; 88–580 g, owls; and 29–458 g, passerines (Dunning 1984). Passerines constituted most of the avian prey.

DISCUSSION

Great Horned Owls are generally considered to be opportunistic feeders, preying on a broader range of species than any other North American owl (Craighead and Craighead 1969, Voous 1988, Marti and Kochert 1996, Houston et al. 1998). Bosakowski and Smith (1992) reported such unusual species as a raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*), and a Red-shouldered Hawk (*Buteo lineatus*); Marti (1974) reported a yellow-bellied marmot and black-tailed prairie dog (*Cynomys ludovicianus*); Errington (1932) reported a striped skunk; and Rudolph (1978) reported a Brazilian free-tailed bat (*Tadarida brasiliensis*). Llinas-Gutierrez et al. (1991) reported a wide variety of arachnids, insects, and reptiles in the owl diet, and Rohner and Doyle (1992) reported a Great Horned Owl feeding on an adult Northern Goshawk (*Accipiter gentilis*).

The moderate trophic niche (high number of prey species unequally distributed [see Methods section]) of the Great Horned Owl reported herein somewhat contrasts with previous studies (see text). Excluding predominately insectivorous owl species, the Great Horned Owl's moderate food-niche breadth (opportunistic feeding) aligns it with species such as the Burrowing Owl (*Speotyto cunicularia*) (Haug et al. 1993), Spotted Owl (*Strix occidentalis*) (Gutierrez et al. 1995), and Eastern Screech-Owl (Gehlbach 1995), for example. Species apparently more opportunistic than Great Horned Owls include the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) (Proudfoot 1997) and Northern Pygmy-Owl (*Glaucidium gnoma*) (Holt and Leroux 1996, Holt and Petersen 2000). More specialized species include the Snowy Owl (*Nyctea scandiaca*) (Watson 1957, Parmelee 1992), Short-eared Owl (*Asio flammeaus*) (Holt 1993, Holt and Leasure 1993), Northern Saw-whet Owl (Holt et al. 1991, Cannings 1993), and Barn Owl (Marti 1989, 1992).

Other *Bubo* species have a trophic niche similar to the Great Horned Owl. Herrera and Hiraldo (1976) reported FNB values ranging from 2.40–6.68 ($\bar{x}$ = 4.13, SD ± 0.01) for the Eurasian Eagle-Owl (*Bubo bubo*) in Europe. Jaksic and Marti (1984) found that Great Horned Owls and Eurasian Eagle-Owls followed a similar trophic pattern in North American and European shrubland. Donázar et al. (1989), however, reported limited dietary convergence between these two species. They attributed discrepancies in trophic diversity to the differences between similar North American and European biomes, variations in the composition and abundance of prey types, and differences in the body masses of Great Horned Owls and Eurasian Eagle-Owls.

The moderate trophic niche of Great Horned Owls could be the result of several factors, including prey species size, diversity, density, availability, and distribution. Marti (1974) suggested that although owls can capture a broad range of prey sizes, an optimum size exists in terms of how efficiently a particular individual prey item can be found and caught. He argued that very small prey is only efficient for Great Horned Owls if it can be caught quickly and easily. Marti felt that prey density, ease of killing, overlap of time of activity between predator and prey, and learning by individual owls all determine what proportions of the diet a particular prey species will comprise.

The Great Horned Owl's moderate food-niche breadth may also reflect the habitat or time of day in which they forage. Open areas the Great Horned Owl inhabits are frequented by mice, voles, lagomorphs, and gophers, which may emerge during the owl's optimal feeding periods of evening, night, and early morning (Maser et al. 1970). The community structure of predators within a particular habitat may also affect food-niche breadth. Marti et al. (1993) found that although predators in an area may utilize prey resources in different fashions, patterns of resource use do emerge, particularly in terms of predator size.

The diet of Great Horned Owls may vary depending upon the particular region the owls inhabit (Marti et al. 1993). Hayward et al. (1993) found that coastal Great Horned Owls in Washington fed exclusively on birds during the summer months. Bosakowski et al. (1989) reported owls living in the deciduous forests of New Jersey, New York, and Connecticut preyed more heavily upon birds than those living in open coniferous forests of the western United States. Desert owls fed on a variety of arachnids, insects, and reptiles because of their availability and abundance in that biome (Jaksic and Marti 1984, Barrows 1989, Llinas-Gutierrez et al. 1991).

Jaksic and Marti (1984) found that the diversity of Great Horned Owl prey at the class level was very low in the temperate regions and very high in the desert regions of North America. They believed this difference reflected the greater representation of mammals in the diet of temperate owls, thus resulting in a moderate trophic niche.

Great Horned Owls may respond opportunistically to the local profile of prey sizes and densities (Jaksic and Delibes 1987, Jaksic 1988). Llina-Gutierrez et al. (1991) suggested that lagomorphs and rodents were the dominant prey species in their study compared with other desert studies in the region because of their high abundance. Rusch et al. (1972) reported that the diet of Great Horned Owls was strongly affected by changes in the numbers of snowshoe hare (*Lepus americanus*). They found that in years with high snowshoe hare populations, owls exhibited higher predation rates on snowshoe hare and lower predation rates on mice and voles.

The data herein support the general conclusion that Great Horned Owls prey on a wide range of species. However, the data also show convincingly that Great Horned Owls feed primarily on only three to four species of voles and mice under most conditions, indicating a moderate food-niche breadth.

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